<u>INCLUSIVE FITNESS</u>

Introduction

Cooperation is abundant throughout the natural world and exists at all biological levels, from genes forming genomes to individuals collaborating in societies. Nature documentaries are frequently packed with stunning examples, from kamikaze bees stinging intruders to save the lives of their nest mates to meerkat helpers feeding the pups of others. However, beneath this appearance of kindness lies one of the most challenging issues for evolutionary theory. The problem is that natural selection favors genes that increase an organism's ability to survive and reproduce and so how can behavior that

benefits others ever evolve? To simplify this problem the complex spectrum of social behaviors can be broken down into pair-wise interactions and classified according to the direct fitness benefits (number of offspring an individual produces stripped of social interactions) and costs to the actors and recipients involved. This leads to four types of behavior: Selfishness (benefit to actor, cost to the recipient) and mutually beneficial interactions (benefit to actor, benefit to the recipient) are easily understood as they increase the direct fitness of the actor. Altruism (cost to the actor, benefit to the recipient) and spite (cost to the actor, cost to the recipient), on the other hand, present an evolutionary paradox—how can a gene that is disadvantageous to an individual spread in a population? Darwin realized this problem, but it wasn't until 1963–1964, when William (Bill) D. Hamilton produced his benchmark papers, that it became clear how actions that decrease direct fitness can evolve through natural selection. Hamilton coined the term "Inclusive Fitness" to emphasize that the quantity that individuals attempt to maximize is not simply direct fitness, but also something called indirect fitness—the effect individuals have on the number of offspring everybody else in the population produces weighted by their relatedness. Inclusive fitness theory remains one of the most active areas of evolutionary research and provides an extremely important tool for understanding both the process and purpose of evolution.

General Overviews

The literature on inclusive fitness is vast, so my recommendations are a few key texts that span the life of the field. There are many more overviews available, and these often appear in the reference lists of the highlighted texts or in other sections of this article. Although the concepts behind inclusive fitness were discussed prior to Hamilton, it was his 1964 contributions (see Hamilton 1964) that provided the foundations of all later work, representing perhaps the most significant contribution to evolutionary biology since Darwin to this day. Amazingly, Hamilton wrote these papers during his PhD at a time when there was still great confusion about what the unit of selection was—genes, individuals, groups, or species? It took over a decade for the magnitude of Hamilton's contribution to be realized, but after this lag research on inclusive fitness grew in three main directions: theory, work on social insects, and work on cooperatively breeding vertebrates (but see *Study Systems*). Although on the surface inclusive fitness theory is quite intuitive, there are many pitfalls. Grafen 1984 clarifies some of the misconceptions and gives directions on how theory can be best used in empirical testing. Trivers 1985 shows how inclusive fitness theory can be used to explain a wide range of evolutionary problems and provides some of the earlier examples across a broad range of taxa. Frank 1998 gives a detailed and easy-to-read account of the somewhat daunting array of concepts and tools used to develop inclusive fitness theory, and Wilson 1975 provides an extensive account of the wonderful natural history of different animal societies. Over the decades since its conception much confusion has arisen over inclusive fitness theory and the study of cooperation, particularly across scientific disciplines. West, et al. 2007 provides a roadmap to navigate through this labyrinth. For general up-to-date reviews of both theory and empirical work see Bourke 2011 and Davies, et al. 2012.

Bourke, A. F. G. 2011. *Principles of social evolution*. Oxford: Oxford Univ. Press. [ISBN: 9780199231157]

A recent review of inclusive fitness theory that shows how it can explain the organization of life through "the major evolutionary transitions" (see *Major Evolutionary Transitions*).

Davies, N. B., J. R. Krebs, and S. A. West. 2012. *An Introduction to Behavioural Ecology*. 4th ed. Oxford: Wiley-Blackwell. [ISBN: 9781444339499]
The latest edition in the series gives an up-to-date account of inclusive fitness theory illustrated with lots of examples. This series of books has formed the backbone of behavioral ecology undergraduate teaching since the 1980s, and it is well worth looking back through past editions.

Frank, S. A. 1998. *Foundations of social evolution*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691059334]
A lucid review of the mathematical methods used to construct inclusive fitness theory. Downloadable from Frank's website.

Grafen, A. 1984. Natural selection, kin selection and group selection. In *Behavioural ecology: An evolutionary approach*. Edited by J. R. Krebs and N. B. Davies, 62–84. Oxford: Blackwell Scientific. [ISBN: 9780632009879]
Outlines what inclusive fitness theory is and how to apply it. Thirty years on this still provides key insight.

Hamilton, W. D. 1964. The genetical evolution of social behaviour I, II. *Journal of Theoretical Biology* 7:1–52.
These papers are the conception of inclusive fitness theory following Hamilton's 1963 short note. The second paper proposes the haplodiploidy hypothesis for the evolution of eusocial insects.

Trivers, Robert. 1985. *Social evolution*. Menlo Park, CA: Benjamin/Cummings. [ISBN: 9780805385076]
This book covers the theoretical basis of inclusive fitness theory and gives great insight into the biological problems it can be applied to, illustrated with weird and wacky examples.

West, S. A., A. S. Griffin, and A. Gardner. 2007. Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology* 20:415–432.
This paper clarifies the confusion that has accumulated over decades of research on social evolution. Helps unify different fields by clearly stating how different terms are used in different disciplines.

Wilson, E. O. 1975. *Sociobiology: The new synthesis*. Cambridge, MA: Harvard Univ. Press. [ISBN: 9780674816213]
When this book was published it became famous for the controversy it caused over its gene-centered discussion of human evolution. However, it is much more than that, providing a comprehensive overview of social evolution at that time. Re-released in 2000 with an extra section on human genetics and neuroscience.

Development of Theory

The initial ideas behind explaining altruism can be traced to Darwin, who realized that in social insects, such as bees, that selection may apply to the family rather than the individual. Intellectual giants such as Fisher, Haldane, Kropotkin, Wright, and Williams, among others, also gave some early thought to solving the problem of altruism. However,

where these greats stalled, Bill Hamilton triumphed. Hamilton was heavily influenced by Fisher's work that combined Darwin's ideas with Mendelian genetics, but he realized this ignored social interactions among genetic relatives. Hamilton showed mathematically that including the effect of social interactions on individual fitness can explain the evolution of altruism and spite (Hamilton 1964 cited under *General Overviews*). To date there have been three main theoretical approaches to modeling how social interactions influence fitness: neighbor-modulated fitness, inclusive fitness, and multilevel selection (reviewed by Wenseleers, et al. 2010). Neighbor-modulated fitness is also referred to as the "direct fitness" approach and in quantitative genetics as "indirect genetic effects" (IGE), and multilevel selection is referred to as "group selection" or "new group" selection. Hamilton 1964 (cited under *General Overviews*) introduced the first two concepts and Hamilton 1975 (cited under *Cooperation between Nonrelatives*) explored multilevel selection, along with Wilson 1975 (cited under *General Overviews*). Hamilton 1996 provides a collection of Hamilton's contributions. After Hamilton identified the importance of indirect fitness benefits for explaining behavior, Maynard Smith 1964 called this "kin selection." The term was readily adopted, and today inclusive fitness theory and kin selection theory are often, although incorrectly, used interchangeably (see Hamilton 1975, cited under *Cooperation between Nonrelatives*, for discussion of the distinction). Group selection has been riddled with confusion (see also *The Price Equation*) and remains to be fully developed but has some advantages to capturing the conflict between individual and group interests (see Okasha 2006 and Wenseleers, et al. 2010). In contrast, the inclusive fitness approach has the advantage of capturing the intuitive notion that individuals are acting to maximize their inclusive fitness and as a result has been much more developed. This has been aided by some key methodological developments such as Taylor and Frank 1996 and Grafen 2006. Recent theory has also been extended to deal with more complex structured populations (see Rousset 2004), frequency dependence, and multilocus and non-additive genetic effects as discussed by Wenseleers, et al. 2010. More generally the history of inclusive fitness theory is outlined in Frank 1998 (cited under *General Overviews*) and Wenseleers, et al. 2010.

Grafen, A. 2006. Optimization of inclusive fitness. *Journal of Theoretical Biology* 238:541–563.
  A theoretical paper that sets out to establish mathematically that individuals act as if to maximize their inclusive fitness. More broadly integrates the mathematical basis of inclusive fitness with that of natural selection and evolutionary adaptation.

Hamilton, W. D. 1996. *Narrow roads of gene land*. Vol. 1, *Evolution of social behaviour*. Oxford: W. H. Freeman/Spektrum. [ISBN: 9780716745303]
  Provides a compilation of Hamilton's papers with an introduction to each one by the man himself that retells tales of the times surrounding when he wrote the papers.

Maynard Smith, J. 1964. Group selection and kin selection. *Nature* 201:1145–1147.
  This paper gives rise to the term "kin selection" and examines the credibility of Wynne-Edwards's ideas about "old" group selection in light of Hamilton's work.

Okasha, S. 2006. *Evolution and the levels of selection*. Oxford: Oxford Univ. Press. [ISBN: 9780199267972]
  A book that reviews and clarifies debates over the level at which selection occurs and that unifies biological and philosophical perspectives.

Rousset, François. 2004. *Genetic structure and selection in subdivided populations*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691088167]

This book provides a comprehensive guide to the mathematical methods used to model evolution in structured populations including inclusive fitness theory. Quite a high level of understanding in population genetics is assumed.

Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *Journal of Theoretical Biology* 180:27–37.

This paper develops the neighbor-modulated/direct fitness method of analyzing inclusive fitness. This opened up new theoretical avenues, as it is a more straightforward method of analyzing inclusive fitness than Hamilton's inclusive fitness formulation.

Wenseleers, T., A. Gardner, and K. R. Foster. 2010. Social evolution theory: A review of methods and approaches. In *Social behaviour: Genes, ecology and evolution*. Edited by T. Székely, A. J. Moore, and J. Komdeur, 132–158. Cambridge, UK: Cambridge Univ. Press. [ISBN: 9780521883177]

A substantial recent review of the different methods used to model social evolution, the way they are interlinked, and their relative merits.

The Price Equation

George Price was a fascinating and troubled character who is well worth reading about (Harman 2010). In Price 1970 and Price 1972, he outlined how any process of selection can be mathematically modeled. This simple equation revolutionized and united many aspects of evolutionary biology, not least social evolution theory. Group selection arguments were, and are still today, pitted against inclusive fitness theory leading to considerable confusion. However, Wade 1985, Frank 1995 and Reeve and Keller 1999 (cited under *Assumptions and Alternative Viewpoints*) discuss how the Price equation provides the formal basis of both inclusive fitness and group selection theory, making it possible to show that the two theories are mathematically equivalent: The two bodies of theory just partition selection in different ways, with inclusive fitness theory drawing a distinction between direct and indirect fitness benefits as opposed to group selection theory, which separates within and between group fitness effects. This has recently been extended by Gardner and Grafen 2009, which uses the Price equation to produce a formal theory of group adaptation following an inclusive fitness approach. The importance of the Price equation in resolving mathematical debate over the differences between inclusive fitness and group selection theory is reviewed by Wenseleers, et al. 2010 (cited under *Development of Theory*) and West, et al. 2008 discusses how useful the two theories have been for understanding empirical findings as well as highlighting Price's contribution to resolving debate.

Frank, S. A. 1995. George Price's contributions to evolutionary genetics. *Journal of Theoretical Biology* 175:373–388.

A summary of the great impact Price had on evolutionary theory written by one of the great evolutionary thinkers.

Gardner, A., and A. Grafen. 2009. Capturing the superorganism: A formal theory of group adaptation. *Journal of Evolutionary Biology* 22:659–671.

This paper uses the Price equation to develop theory where the group acts to maximize its inclusive fitness rather than the individual. This shows the force of the Price

equation in unifying different approaches and illustrates that under limited circumstances groups can be thought of as individuals—"superorganisms."

Harman, O. 2010. *The Price of altruism: George Price and the search for the origins of kindness*. London: Bodley Head. [ISBN: 9781847920621]

A biography of Price that won the *LA Times* Book Prize.

Price, G. R. 1970. Selection and covariance. *Nature* 227:520–521.

This small paper had a large impact. Price presented his equation and its application in modeling selection in general, but with particular reference to genetic selection.

Price, G. R. 1972. Extension of covariance selection mathematics. *Annuals of Human Genetics* 35:485–490.

An extension of his 1970 contribution where he applies his equation to group selection and selection in populations with overlapping generations.

Wade, M. J. 1985. Soft selection, hard selection, kin selection, and group selection. *American Naturalist* 125:61–73.

This paper demonstrates, using the Price equation, how different models of selection in structured populations, including group selection and inclusive fitness theory, are closely related.

West, S. A., A. S. Griffin, and A. Gardner. 2008. Social semantics: How useful has group selection been? *Journal of Evolutionary Biology* 21:374–385.

A response to criticisms by D. S. Wilson that examines the differences between group selection and inclusive fitness theory, the way they are unified by the Price equation, and their relative merits for understanding empirical patterns.

Hamilton's Rule

The essence of inclusive fitness theory is neatly captured by Hamilton's rule, which states that genes for a particular behavior or trait will be favored by natural selection when $rb - c > 0$, where c is the direct fitness cost to the actor, b is the direct fitness benefit to the recipient, and r is genetic relatedness between actors and recipients (Hamilton 1964, cited under *General Overviews*). Perhaps most important, Hamilton's rule has led to strong links between theory and empirical testing—one of the great triumphs of inclusive fitness theory is that it can easily be applied to data (see Grafen 1984 cited under *General Overviews* and West, et al. 2008 cited under *The Price Equation*). However, the devil is in the details, and the terms require careful definition (Grafen 1984, cited under *General Overviews* and West, et al. 2007, cited under *General Overviews*). The benefits and costs are measured in terms of lifetime reproductive success *not* other units, such as energy, or over other timescales, as this can lead to confusion between terms such as altruism and reciprocal altruism as discussed by West, et al. 2007 cited under *General Overviews*. Often relatedness is considered to be the probability of identity by descent, but Hamilton realized that the appropriate measure of r in this context is genetic similarity of actors and recipients relative to the population average. This was highlighted in his 1970 reformulation and by Grafen 1985. Measuring relatedness with respect to the population average means that relatedness can also be negative—individuals share fewer genes than on average for the population—and Hamilton 1970 showed that this can explain the evolution of spite. Another important realization about the definition of relatedness came in the 1990s when Taylor 1992 showed that competition between relatives can completely cancel out the indirect fitness benefits of helping. Ways of

accounting for competition between relatives came in two forms. First, Queller 1994 showed this can be incorporated by measuring relatedness among the group of individuals that compete (according to the "scale of competition") not the global population. This method has the advantage of highlighting that relatedness is a relative measure and easily shows how empirical work can over estimate relatedness, but it can be difficult to correctly define the scale of competition (Gardner and West 2004). Second, Frank 1998 (cited under *General Overviews*) showed that competition between relatives can be accounted for by adjusting the benefits of helping according to the scale of competition. More generally, Davies, et al. 2012 (cited under *General Overviews*) gives a recent review of empirical applications of Hamilton's rule.

Gardner, A., and S. A. West. 2004. Spite and the scale of competition. *Journal of Evolutionary Biology* 17:1195–1203.

This review covers the importance of the scale of competition in inclusive fitness theory and shows how local competition can favor the evolution of spite.

Grafen, A. 1985. A geometric view of relatedness. In *Oxford surveys in evolutionary biology*. Vol. 2. Edited by Richard Dawkins and M. Ridley, 28–89. Oxford: Oxford Univ. Press. [ISBN: 9780198541745]

This paper uses the Price equation to prove Hamilton's rule and shows the importance of measuring relatedness relative to the population average.

Hamilton, W. D. 1970. Selfish and spiteful behaviour in an evolutionary model. *Nature* 228:1218–1220.

A concise paper in which Hamilton focuses on harmful interactions as opposed to altruism and derives Hamilton's rule using the Price equation.

Queller, D. C. 1994. Genetic relatedness in viscous populations. *Evolutionary Ecology* 8:70–73.

This paper shows how the results of Hamilton's rule when relatives compete can be restored if relatedness is measured among competing individuals.

Taylor, P. D. 1992. Altruism in viscous populations—an inclusive fitness model. *Evolutionary Ecology* 6:352–356.

An influential paper that followed simulation work by Wilson 1992 showing how indirect fitness benefits can be cancelled out by competition between relatives.

Cooperation between Nonrelatives

Inclusive fitness provides an extremely general theory of evolution and not just interactions between relatives—a common misunderstanding perhaps because of the mix-up with kin selection (see Hamilton 1975). It provides a framework for understanding the evolution of cooperation between nonrelatives by summarizing the direct fitness benefits of social interactions. Trivers 1971 examines when cooperation between nonrelatives evolves through mutual benefits (within species interactions) and mutualisms (between species interactions). West Eberhard 1975 and Sachs, et al. 2004 provide early and more recent reviews, respectively, of explanations for cooperation between nonrelatives, as well as relatives, whereas Hammerstein 2003 and Clutton-Brock 2009 focus more exclusively on cooperation between nonrelatives. Recent work has illustrated that there are a variety of mechanisms that can maintain cooperation between nonrelatives, and it can be informative to distinguish between them. These mechanisms include both enforced cooperation such as "paying rent" and "worker policing" and nonenforced

cooperation such as "the selfish herd" and "group augmentation"; this has been reviewed in a number of places—see West, et al. 2007 and Davies, et al. 2012 (cited under *General Overviews*). The great benefit of inclusive fitness theory is that in reality social groups are often made up of unrelated and related individuals, and it allows the relative importance of direct and indirect benefits in driving cooperation to be quantified.

Clutton-Brock, T. H. 2009. Cooperation between non-kin in animal societies. *Nature* 462:51–57.

A review article that examines the mechanisms explaining cooperation between nonrelatives, particularly mammals.

Hamilton, W. D. 1975. Innate social aptitudes of man: An approach from evolutionary genetics. In *Biosocial Anthropology*. Edited by R. Fox, 133–155. New York: Wiley. [ISBN: 9780470270332]

In this book chapter Hamilton examines what the apparent purpose of natural selection is and how cooperation can evolve in humans both through direct and indirect fitness benefits. He also discusses the differences between kin selection and inclusive fitness and their relationship to levels of selection.

Hammerstein, P. 2003. *Genetic and cultural evolution of cooperation*. Cambridge, MA: MIT Press. [ISBN: 9780262083263]

A broad overview of the mechanisms and processes that promote cooperation other than relatedness across different biological levels from molecules to societies.

Sachs, J. L., U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. The evolution of cooperation. *Quarterly Review of Biology* 79:135–160.

A general review of explanations of cooperation based on both direct and indirect fitness benefits.

Trivers, R. L. 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46:35–57.

A benchmark paper in which Trivers outlines his ideas on the importance of reciprocal direct benefits for the evolution of cooperation.

West, S. A., A. S. Griffin, and A. Gardner. 2007. Evolutionary explanations for cooperation. *Current Biology* 17:R661–R672.

A concise review that maps out the mechanisms that maintain cooperation between both relatives and nonrelatives.

West Eberhard, M. J. 1975. The evolution of social behavior by kin selection. *Quarterly Review of Biology* 50:1–33.

One of the first reviews of inclusive fitness theory to include discussion of interaction between nonrelatives and relatives with particular reference to the hyplodiploidy hypothesis.

Kin Discrimination

Indirect fitness benefits depend on relatives interacting, which can happen in three main ways (see Sherman, et al. 1997). First, limited dispersal can lead to a build up of relatedness amongst individuals. This is discussed by Hamilton 1964 (cited under *General Overviews*), is reviewed by Hatchwell 2010, and was experimentally tested by Griffin, et al. 2004. Second, individuals can use environmental cues, such as who they grew up with (associative learning/familiarity), or match similarity in traits of unknown individuals to known relatives to determine relatedness (phenotype matching). There is

extensive evidence for environmental cues being the most important mechanism of kin discrimination, which is reviewed by Komdeur, et al. 2008; Widdig 2007; and d'Ettorre and Lenoir 2010. Third, genetic kin recognition can be used to discriminate between related and unrelated individuals. Hamilton first highlighted that indirect fitness benefits depend on genetic relatedness at a particular locus, not kinship or relatedness across the whole genome. This potentially results in selection for genes or tightly linked sets of genes that do three things: produce a conspicuous phenotype (e.g., a "green beard"; see Dawkins 1976), recognize the gene in other individuals, and direct help toward those individuals. Rousset and Roze 2007 provides recent theoretical insight into the conditions favoring the evolution of recognition alleles, and Bourke 2011 (cited under *General Overviews*) provides an overview of why they are rare with a summary of the few cases where they have been found.

D'Ettorre, P., and A. Lenoir. 2010. Nestmate recognition. In *Ant ecology*. Edited by L. Lach, C. L. Parr, and K. L. Abbott, 194–209. Oxford: Oxford Univ. Press. [ISBN: 9780199544639]
Reviews the evidence of nest mate discrimination across the social insects.

Dawkins, Richard. 1976. *The selfish gene*. Oxford: Oxford Univ. Press. [ISBN: 9780198575191]
A popular science account of inclusive fitness theory that Dawkins used to present his gene-centered view of evolution. The latest edition was published in 2006.

Griffin, A. S., S. A. West, and A. Buckling. 2004. Cooperation and competition in pathogenic bacteria. *Nature* 430:1024–1027.
The first experimental demonstration of the importance of dispersal and the scale of competition for the evolution of cooperation.

Hatchwell, B. J. 2010. Cryptic kin selection: Kin structure in vertebrate populations and opportunities for kin-directed cooperation. *Ethology* 116:203–216.
A review of the causes and consequences of kin structure in cooperatively breeding vertebrates.

Komdeur, J., D. S. Richardson, and B. Hatchwell. 2008. Kin-recognition mechanisms in cooperative breeding systems: Ecological causes and behavioral consequences of variation. In *The ecology of social evolution*. Edited by Judith Korb and J. Heinze, 175–193. Berlin: Springer-Verlag. [ISBN: 9783540759560]
Reviews evidence of the amount of help provided in relation to relatedness in cooperatively breeding birds.

Rousset, F., and D. Roze. 2007. Constraints on the origin and maintenance of genetic kin recognition. *Evolution* 61:2320–2330.
A theoretical paper examining the evolutionary stability of genetic kin recognition systems that highlights the importance of balancing selection for maintaining genetic variation at recognition loci.

Sherman, P. W., H. K. Reeve, and D. W. Pfennig. 1997. Recognition systems. In *Behavioural ecology: An evolutionary approach*. 4th ed. Edited by John R. Krebs and N. B. Davies, 69–96. Oxford: Blackwell Science. [ISBN: 9780865427310]
This book chapter gives a more general overview of the evolution of recognition systems, which feature kin discrimination.

Widdig, A. 2007. Paternal kin discrimination: The evidence and likely mechanisms. *Biological Reviews* 82:319–334.

Reviews the evidence for different kin discrimination mechanisms with particular focus on paternal care in primates.

Ecology

Ecology is implicit in inclusive fitness theory having a crucial influence on all the components of Hamilton's rule. In particular the way ecology constrains independent breeding ("Ecological Constraints" hypothesis; see Emlen 1982) has been a focus of vertebrate research and to a lesser extent invertebrates, but see Crozier and Pamilo 1996 and Davies, et al. 2012 (cited under *General Overviews*) for insect work. Hatchwell and Komdeur 2000 provides a summary of the different ecological factors that may constrain independent breeding and promote cooperation. The way ecology constrains independent breeding and influences the benefits and costs of helping has also been extensively studied through reproductive skew theory. Skew theory focuses on explaining the distribution of reproductive success across adults in social groups; in some species this is fairly even (low skew) while in others reproduction is monopolized by a few individuals (high skew). Skew theory was kick-started by Sandra Vehrencamp, who used Hamilton's rule to show that high relatedness may explain high skew. Later developments were presented by Reeve and Ratnieks 1993, and subsequently a huge number of models were produced that explored how different ecological conditions influenced skew. For a general overview see Hager and Jones 2009. Ecology also determines patterns of relatedness through changing population structure and patterns of dispersal, which is outlined in Rousset 2004 (cited under *Development of Theory*). More generally, Koenig and Dickinson 2004 reviews the role of ecology in cooperatively breeding birds, Wong and Balshine 2011 examines fish, and Solomon and French 1997 discusses mammalian societies.

Crozier, R. H., and P. Pamilo. 1996. *Evolution of social insect colonies: Sex allocation and kin selection*. Oxford: Oxford Univ. Press. [ISBN: 9780198549437]
   This book provides an extensive review of the application of inclusive fitness theory to the social insects.

Emlen, S. T. 1982. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119:29–39.
   The conception of the ecological constraints hypothesis for the evolution of cooperative breeding.

Hager, R., and C. B. Jones. 2009. *Reproductive skew in vertebrates: Proximate and ultimate causes*. Cambridge, UK: Cambridge Univ. Press. [ISBN: 9780521864091]
   A comprehensive recent review of the theory, mechanisms, and future directions of the field of reproductive skew.

Hatchwell, B. J., and J. Komdeur. 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* 59:1079–1086.
   An overview of the empirical evidence for the ecological constraints hypothesis and the influence of life-history variation on the occurrence of cooperative breeding.

Koenig, W. D., and J. L. Dickinson, eds. 2004: *Ecology and evolution of cooperative breeding in birds*. Cambridge, UK: Cambridge Univ. Press. [ISBN: 9780521822718]
   A guide to research on cooperatively breeding birds that covers the many aspects of their behavior, physiology, genetics, and even conservation.

Reeve, H. K., and F. Ratnieks. 1993. Queen-queen conflicts in polygynous societies: Mutual tolerance and reproductive skew. In *Queen number and sociality in insects*. Edited by L. Keller, 45–85. Oxford: Oxford Univ. Press. [ISBN: 9780198540571]
An extension of Vehrencamp's 1983 model that explains variation in reproductive skew across social insects using inclusive fitness theory.
Solomon, N. G., and J. A. French. 1997. *Cooperative breeding in mammals.* Cambridge, UK: Cambridge Univ. Press. [ISBN: 9780521454919]
This book is similar in approach to Koenig and Dickinson 2004, providing a general overview of the empirical work on the biology of cooperatively breeding mammals.
Wong, M., and S. Balshine. 2011. The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher*. *Biological Reviews* 86.2: 511–530.
This paper examines different explanations for cooperation in the most intensively studied species of cooperatively breeding fish.

The Power of Inclusive Fitness Theory

Inclusive fitness theory has triumphed in many areas of evolutionary biology. Subsections provide introductions into some areas where inclusive fitness theory has proved particularly useful.

Major Evolutionary Transitions

The organization of life on earth is often viewed from the perspective of taxonomic hierarchy. However, a more conceptual way of examining biological complexity is through the "major transitions," a term coined by Maynard Smith and Szathmáry 1995. Each major transition requires independent units to join to form a more complex life form that can only replicate as one. For example, genes join to form genomes, unicells form multicellular organisms, and individuals form eusocial societies. Inclusive fitness theory has provided great insight into these transitions, which are discussed by Dawkins 1982 and Bourke 2011 (cited under *General Overviews*). Queller 2000 draws a distinction between transitions that have involved relatives ("fraternal") and nonrelatives ("egalitarian"), further clarifying the importance of inclusive fitness theory. The evolutionary transition to multicellularity is discussed by Michod 2007 and Grosberg and Strathmann 2007, and for a recent comparative analysis see Fisher, et al. 2013. Boomsma 2009 examines the transition to eusociality and draws parallels with the transition to multicellularity. The author argues that "monogamy" or "lifetime commitment" is the key condition that must be met for the major transition to eusociality and multicellularity to occur ("the monogamy hypothesis," following on from initial ideas by Charnov). Boomsma demonstrates that under lifetime monogamy, relatedness to potential offspring is equal to siblings so only a small ecological benefit of helping raise siblings is needed for altruism to evolve, and over longer timescales this can result in major transitions. Boomsma's work has also helped resolve debate over the importance of haplodiploid genetics of many eusocial insects (Hamilton's haplodiploidy hypothesis; see West Eberhard 1975 cited under *Cooperation between Nonrelatives*), now generally regarded to be of minimal importance for the evolution of eusociality.
Boomsma, J. J. 2009. Lifetime monogamy and the evolution of eusociality. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364.1533: 3191–3207.

This paper provides an extension of Boomsma's 2007 article, outlining the monogamy hypothesis more fully, reviewing current empirical evidence, and applying the same ideas to the evolution of multicellularity.

Dawkins, R. 1982. *The extended phenotype: The gene as the unit of selection*. Oxford: W. H. Freeman. [ISBN: 9780716713586]
Discusses how conflict suppression via high relatedness is important in the evolution of multicellularity.

Fisher, R. M., C. K. Cornwallis, and S. A. West. 2013. Group formation, relatedness and the evolution of multicellularity. *Current Biology* 23:1120–1125.
A comparative analysis that demonstrates high relatedness has been a key requirement in multiple independent evolutionary transitions to complex multicellularity.

Grosberg, R. K., and R. R. Strathmann. 2007. The evolution of multicellularity: A minor major transition? *Annual Review of Ecology, Evolution and Systematics* 38:621–654.
This review examines the evolutionary transition to multicellularity from an inclusive fitness perspective.

Maynard Smith, J., and E. Szathmáry. 1995. *The major transitions in evolution*. Oxford: W. H. Freeman. [ISBN: 9780716745259]
This book presents the different major evolutionary transitions and how they have been favored by natural selection.

Michod, R. E. 2007. Evolution of individuality during the transition from unicellular to multicellular life. *Proceedings of the National Academy of Sciences of the United States of America* 104:8613–8618.
This paper examines the concept of individuality and reviews experimental work, primarily on volvox, that has shown transitions to multicellularity are favored by high relatedness and costs of reproduction.

Queller, D. C. 2000. Relatedness and the fraternal major transitions. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 355:1647–1655.
This paper uses inclusive fitness theory to draw the distinction between transitions that have involved related and nonrelated replicating units.

Conflict and Spite

Hamilton was initially motivated by explaining altruism, but also showed that inclusive fitness theory can be used to explain levels of conflict (Hamilton 1964 cited under *General Overviews*). In Hamilton 1979, he illustrated this with examples of insects, such as fig wasps and mites, where relatedness negatively correlated with levels of fighting. Interestingly, some of these initial results were later overturned when it was found that extreme local competition between relatives reduced the indirect benefits of being less aggressive (see *Hamilton's Rule*). Nevertheless, inclusive fitness theory has been particularly influential in identifying where potential conflict should arise, for instance due to variation in relatedness within groups, and the conditions where this leads to actual conflict. Frank 2003 and Ratnieks, et al. 2006 review theory and empirical examples from social insects of conflict and its resolution. Conflict within vertebrate species has also been extensively studied, especially from the perspective of reproductive suppression, which is discussed in Hager and Jones 2009 (cited under *Ecology*). Conflict can occur between descendant and non-descendant kin, and Trivers 1974 focuses

on descendant kin using inclusive fitness theory to formulate ideas on parent-offspring conflict (also known as "parental investment" theory). This was later reviewed by Mock and Parker 1997, which also discusses conflict between non-descendant kin using examples mainly from birds, but with some discussion of mammals, insects, and plants. Finally, one especially nasty type of conflict that has gained recent attention is spite. Hamilton also realized that this could be explained by inclusive fitness theory (Hamilton 1970 cited under *Hamilton's Rule*). Explaining why individuals would harm others at a cost to themselves posed as big a problem for evolutionary theory as did altruism. After some confusion, it turns out that spite can evolve when the harm inflicted on a negatively related individual (less related than the population average—see Grafen 1985 cited under *Hamilton's Rule*) benefits a third party that is positively related—altruism toward a third party. Overviews of spite are provided by Foster, et al. 2001; Gardner and West 2004 (cited under *Hamilton's Rule*); and West and Gardner 2010.

Foster, K., T. Wenseleers, and F. Ratnieks. 2001. Spite: Hamilton's unproven theory. *Annales Zoologici Fennici* 38:229–238.
  A review of the history and meaning of spite that illustrates how evidence of spite often has a more parsimonious interpretation.

Frank, S. A. 2003. Perspective: Repression of competition and the evolution of cooperation. *Evolution* 57.4: 693–705.
  A theoretical review of how inclusive fitness theory can explain reductions in conflict through coercion and selfish restraint.

Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects. In *Sexual selection and reproductive competition in insects*. Edited by M. S. Blum and N. A. Blum, 167–220. New York: Academic Press. [ISBN: 9780121087500] [class:conference-paper]
  Based in part on papers presented at the 15th International Congress of Entomology held in Washington, D.C. in 1976. Comparative evidence that high relatedness reduces conflict in invertebrates.

Mock, D. W., and G. A. Parker. 1997. *The evolution of sibling rivalry*. Oxford: Oxford Univ. Press. [ISBN: 9780198577430]
  This book presents an overview of conflict within the family unit, including parent-offspring and sibling conflict.

Ratnieks, F. L. W., K. R. Foster, and T. Wenseleers. 2006. Conflict resolution in insect societies. *Annual Review of Entomology* 51:581–608.
  A review of the different types of conflict within insect societies.

Trivers, R. L. 1974. Parent-offspring conflict. *American Zoologist* 14:249–264.
  The conception of Trivers's influential theory of parent-offspring conflict.

West, S. A., and A. Gardner. 2010. Altruism, spite, and greenbeards. *Science* 327:1341–1344.
  A recent review that includes discussion on theoretical and empirical evidence for spite.

Sex Allocation

Inclusive fitness theory has been instrumental in explaining variation in the amount individuals invest in male versus female offspring—sex allocation. Research on sex allocation is one of the great triumphs of evolutionary biology being able to explain, across extremely diverse taxa, both the number (sex ratios) and the amount invested in

male versus female offspring. Darwin initially realized that the prevalence of equal sex ratios needed explaining, but it wasn't until Fisher 1930 that an answer was provided. The next major development was not until Hamilton 1967, which showed that inclusive fitness theory could explain biased sex ratios when brothers compete for mates. Hamilton called this process local mate competition. Trivers and Willard 1973 also examines the role of ecology in determining sex allocation using inclusive fitness theory to predict how investment in male and female offspring should change with environmental variation. Trivers and Hare 1976 also shows how sex allocation could lead to conflict within social groups. The authors integrated the work of Fisher 1930 and Hamilton 1964 (cited under *General Overviews*) with parent-offspring conflict theory to show that in social insects the interests of workers and queens differed with respect to the sex ratio of the brood— queens are equally related to male and female offspring, whereas for workers relatedness to sisters is three time higher than to males. However, it was Charnov 1982 that gave rise to the cohesive field of sex allocation that exists today. After Charnov there was great interest in the field and in particular Taylor and Frank (see Taylor and Frank 1996 cited under *Development of Theory*) greatly developed theory on sex allocation using an inclusive fitness framework, which was synthesized by Frank 1998 (cited under *General Overviews*). For a recent and thorough overview of the history, theory, and empirical work on sex allocation see West 2009.

Charnov, E. L. 1982. *The theory of sex allocation*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691083117]
  The first synthesis of theoretical and empirical research on sex allocation theory.

Fisher, R. 1930. *The genetical theory of natural selection*. Oxford: Clarendon.
  One of the most important texts in evolutionary biology—it put Darwin's ideas on a solid mathematical footing. As relevant today as it has ever been. Packed with insight including Fisher's theory of equal sex ratios.

Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477–488.
  A landmark paper that introduces the concepts of local mate competition and the theoretical basis to sex ratio evolution.

Trivers, R. L., and H. Hare. 1976. Haplodiploidy and the evolution of the social insect. *Science* 191:249–263.
  A key paper that integrates the parent-offspring conflict of Trivers 1974 (cited under *Conflict and Spite*) with Hamilton 1964 (cited under *General Overviews*) to reveal potential conflict between workers and queen in social insects.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92.
  A theoretical paper that examines how investment in male and female offspring should change with environmental conditions, the costs of producing offspring, and maternal condition. A paper that has led to extensive empirical work.

West, S. A. 2009. *Sex allocation theory*. Princeton, NJ: Princeton Univ. Press. [ISBN: 9781400832019]
  The second synthesis of theoretical and empirical research on sex allocation theory.

Mating Patterns

Inclusive fitness theory is clearly important for understanding interactions between reproductive competitors, but has also been useful for understanding interactions between

sexual partners. Specifically, it has contributed to explaining patterns of inbreeding, multiple mating, and sexual conflict. When inbreeding reduces inclusive fitness, and the probability of encountering related sexual partners is sufficiently high, selection can favor inbreeding avoidance, for instance through dispersal (see Hamilton and May 1977). Parker 1979 and Smith 1979 further demonstrated that there may be sexual conflict over inbreeding when the direct fitness benefits of additional matings (usually males) outweigh reductions in indirect fitness caused by decreasing the fitness of the related partner in one sex more than the other. This was later shown by Perrin and Mazalov 2000 to be important for explaining sex-biased dispersal. Inclusive fitness theory has also clarified how female mating behavior influences the evolution of cooperation and how cooperation influences female mating behavior. Consistent with the monogamy hypothesis (see *Major Evolutionary Transitions*), female lifetime monogamy has preceded the evolution worker castes in all lineages of eusocial insects (see Boomsma 2009 cited under *Major Evolutionary Transitions*). However, dense congregations of highly related individuals, such as those in social insect colonies, can increase the risk of disease outbreaks. This in turn can select for female multiple mating to increase genetic diversity in colonies (see Hamilton 1996 cited under *Development of Theory*, Schmid-Hempel and Crozier 1999, and van Baalen and Beekman 2006). More broadly, inclusive fitness theory provides a framework for understanding all sexual interactions, which is covered by Bourke 2009 and Pizzari and Gardner 2012.

Bourke, A. F. G. 2009. The kin structure of sexual interactions. *Biology Letters* 5.5: 689–692.
  A concise overview of how inclusive fitness theory can be used to understand interactions between sexual partners.

Hamilton, W. D., and R. May. 1977. Dispersal in stable habitats. *Nature* 269:578–581.
  A theoretical examination of dispersal strategies with respect to environmental variation and risks of inbreeding.

Parker, G. A. 1979. Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects*. Edited by M. S. Blum and N. A. Blum, 123–166. New York: Academic Press. [ISBN: 9780121087500] [class:conference-paper]
  Based in part on papers presented at the 15th International Congress of Entomology held in Washington, D.C. in 1976. A very influential paper that outlines the basis of sexual conflict including conflict over inbreeding.

Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *American Naturalist* 155:116–127.
  This paper uses an inclusive fitness approach to examine patterns of sex-biased dispersal with respect to different probabilities of inbreeding and female multiple mating.

Pizzari, T., and A. Gardner. 2012. The sociobiology of sex: Inclusive fitness consequences of inter-sexual interactions. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* 367:2314–2323.
  A recent review of the way interactions between sexual partners can be understood using inclusive fitness theory.

Schmid-Hempel, P., and R. H. Crozier. 1999. Polyandry versus polygyny versus parasites. *Philosophical Transactions of the Royal Society of London Series B:Biological Sciences* 354:507–515.

A comparative study that shows low relatedness was associated with lower parasite loads.

Smith, R. H. 1979. On selection for inbreeding in polygynous animals. *Heredity* 43:205–211.
This paper uses an inclusive fitness approach to explain the absence of inbreeding avoidance.
Van Baalen, M., and M. Beekman. 2006. The costs and benefits of genetic heterogeneity in resistance against parasites in social insects. *American Naturalist* 167:568–577.
An overview of the links between mating system, genetic diversity, and disease susceptibility in social insects.

Parasite Virulence

Inclusive fitness theory has made clear predictions about the evolution of parasite virulence. When hosts are infected with multiple strains of genetically distinct pathogens, which often occurs, genetic relatedness between the strains determines levels of competition and cooperation. In turn the level of competition between pathogens can both increase and decrease virulence depending on the details of the host parasite systems. The application of inclusive fitness theory to parasite virulence is reviewed in Frank 1996. For a more general overview of host-pathogen interactions with some discussion of inclusive fitness theory see Dieckmann, et al. 2005 (e.g., chapter 12) and for a recent review of empirical evidence and theoretical predictions see Buckling and Brockhurst 2008. Wild, et al. 2009 uses inclusive fitness theory to clarify why parasite virulence is predicted to decline with increased relatedness between pathogens.

Buckling, A., and M. A. Brockhurst. 2008. Kin selection and the evolution of virulence. *Heredity* 100:484–488.
A review that examines the evolution of parasite virulence from an inclusive fitness perspective.
Dieckmann, U., J. A. J. Metz, M. W. Sabelis, and K. Sigmund. 2005. *Adaptive dynamics of infectious diseases: In pursuit of virulence management.* New York: Cambridge Univ. Press. [ISBN: 9780521022132]
This book provides a general overview of how evolutionary theory, including inclusive fitness theory, can be used in the management of infectious diseases.
Frank, S. A. 1996. Models of parasite virulence. *Quarterly Review of Biology* 71:37–78.
A review of the theoretical approaches used for understanding parasite virulence.
Wild, G., A. Gardner, and S. A. West. 2009. Adaptation and the evolution of parasite virulence in a connected world. *Nature* 459:983–986.
This paper examines how dispersal rates can influence relatedness structure and in turn the evolution of virulence. A number of competing explanations for the mechanistic basis of the link between pathogen relatedness and virulence are investigated.

Study Systems

Inclusive fitness theory has provided insight into a diverse set of problems in a diverse set of taxa. Original work focused on social insects, and this is reviewed by Wilson 1975 (cited under *General Overviews*) and Crozier and Pamilo 1996 (cited under *Ecology*). Slightly later, research on cooperative breeding vertebrates, namely birds and mammals, gathered speed. Studies on birds were analyzed by Brown 1987 and

Koenig and Dickinson 2004 (cited under *Ecology*), general mammal work is reviewed by Clutton-Brock 2009, and the substantial body of work that has accumulated on cooperation in humans is examined by Hammerstein 2003 (cited under *Cooperation between Nonrelatives*), Sigmund 2007, and Boyd and Richerson 2009. Fish have also been studied, but to a much lesser extent (see Wong and Balshine 2011 cited under *Ecology*). However, experimental tests of evolutionary processes in both social insects and cooperative breeding vertebrates are extremely difficult, if not impossible. As a result, new systems have been developed, and in particular experimental evolution experiments on microorganisms have proved particularly useful for testing inclusive fitness theory (see West, et al. 2006).

Brown, J. L. 1987. *Helping and communal breeding in birds: Ecology and evolution.* Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691084572]

An early overview of research on cooperatively breeding birds.

Boyd, R., and P. Richerson. 2009. Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3281–3288.

A review of research on cooperation in humans.

Clutton-Brock, T. 2009. Structure and function in mammalian societies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364:3229–3242.

Provides a general overview of the evolution of reproductive strategies in mammalian societies with an emphasis on inclusive fitness theory.

Sigmund, K. 2007. Punish or perish? Retaliation and collaboration among humans. *Trends in Ecology and Evolution* 22:593–600.

This review discusses the importance of reciprocity and enforcement for cooperation in humans.

West, S. A., A. S. Griffin, A. Gardner, and S. P. Diggle. 2006. Social evolution theory for microbes. *Nature Reviews Microbiology* 4:597–607.

Provides a detailed account of the biology of microorganisms and their many advantages for testing inclusive fitness theory.

Assumptions and Alternative Viewpoints

Inclusive fitness theory has been surrounded by debate since its conception. Dawkins 1979 gives a summary of the early discussions. More recent debate has been over the mathematical techniques underlying theory. In particular, inclusive fitness theory has been criticized as it makes three key assumptions: first, that costs and benefits are additive not multiplicative. Second, that benefits and costs are not genotype specific. Charlesworth 1978 points out that if a dominant allele causes its carrier to commit suicide to benefit its relatives then all individuals carrying this gene would die and the altruistic gene would go extinct. Third, selection is weak. If selection is strong then genes under selection will have lower allele frequencies than genes not under strong selection and this will mean that r is different for different genes across the genome. These assumptions and the problems they cause are discussed by Grafen 1984 (cited under *General Overviews*); Wenseleers, et al. 2010 (cited under *Development of Theory*); and Gardner, et al. 2011. The debate over whether group or multilevel selection is a more appropriate method for modeling the evolution of eusociality has also been based on such assumptions. See Nowak, et al. 2010 and corresponding replies, e.g., Abbot, et al. 2010,

for later discussions. Despite these debates rumbling on, Reeve and Keller 1999 points out (some time ago) that such debate lacks any real foundation (see also Wenseleers, et al. 2010 cited under *Development of Theory*).

Abbot, P., J. Abe, J. Alcock, S. Alizon, et al. 2011. Inclusive fitness theory and eusociality. *Nature* 471.7339: E1–E4.

A rebuttal by an extensive list of authors to the criticisms of inclusive fitness theory raised by Nowak, et al. 2010. Specifically, the paper clarifies the link between inclusive fitness and natural selection theory, the assumptions made by inclusive fitness theory, and the biological insight it has provided.

Charlesworth, B. 1978. Some models of the evolution of altruistic behaviour between siblings. *Journal of Theoretical Biology* 72:297–319.

This paper examines inclusive fitness theory from a population genetics perspective and provides some key discussion of the theoretical assumptions.

Dawkins, R. 1979. Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie* 51:184–200.

This paper provides an outline of some of the early misunderstandings of inclusive fitness theory.

Gardner, A., S. A. West, and G. Wild. 2011. The genetical theory of kin selection. *Journal of Evolutionary Biology* 24:1020–1043.

This paper presents a defense against criticisms that inclusive fitness theory makes overly restrictive assumptions.

Nowak, M. A., C. E. Tarnita, and E. O. Wilson. 2010. The evolution of eusociality. *Nature* 466:1057–1062.

The authors put forward a case against inclusive fitness theory and present what they describe as an alternative theory for the evolution of eusociality. See also the many rebuttals that were later published online by *Nature*. It's worth noting that Wilson started his career as a great supporter of inclusive fitness theory.

Reeve, H. K., and L. Keller. 1999. Levels of selection: Burying the units-of-selection debate and unearthing the crucial new issues. In *Levels of selection in Evolution*. Edited by L. Keller, 3–14. Princeton, NJ: Princeton Univ. Press. [ISBN: 9780691007038]

Outlines the debate over levels of selection and discusses why it is futile.